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COMPARATIVE ANALYSIS OF THE DIET OF THE LONG-BEAKED COMMON DOLPHIN (*DELPHINUS CAPENSIS*) WITH THREE OTHER SMALL CETACEANS OFF CENTRAL PERU

Ignacio García-Godos [#], Koen Van Waerebeek, Julio C. Reyes [*] and Joanna Alfaro [+]

Peruvian Centre for Cetacean Research (CEPEC), MUSEO DE LOS DELFINES, Pucusana, Peru
Contact e-mail: cepec.dir@terra.com.pe

Current addresses :
 # Area de Aves y Mamíferos Marinos, Instituto del Mar del Perú (IMARPE), Apdo 22, Callao, Peru
** Areas Costeras y Recursos Marinas (ACOREMA) Av. San Martín 1471, Pisco, Pisco, Peru*
+ Asociación ProDelphinus, Jirón Octavio Bernal 572-5, Lima 11, Peru

ABSTRACT

The diet of long-beaked common dolphin *Delphinus capensis*, dusky dolphin *Lagenorhynchus obscurus*, Burmeister's porpoise *Phocoena spinipinnis*, and bottlenose dolphin *Tursiops truncatus*, was determined based on 281 stomach contents collected along the Peruvian central coast and San Juan de Marcona in the period 1987-1993. Counts of otoliths, squid beaks and some other remains were used to estimate frequency of occurrence and prey percentage of composition (PC). Long-beaked common dolphins (n=117) fed mainly on fish (98.71% of preys), the remainder was composed of squids and crustaceans: Peruvian anchovies *Engraulis ringens* (PC= 71.14%), *Vincigerria lucetia* (7.89%), *Lampanictus parvicauda* (6.77%), *Merluccius gayi* (4.49%), *Odontesthes regia* (3.54%), *Mictophum nitidulum* (2.62%) and *Trachurus picturatus* (1.42%). Dusky dolphins (n=66) consumed *E. ringens* (49.8%, 16.9%), *L. parvicauda* (23.6%, 0.1%), *T. picturatus* (17.1%, 0%), *Normachthys crockeri* (0%, 76.4%), *V. lucetia* (3.5%, 0.1%), and *Sardinops sagax* (2.8%, 0 %) off the central Peruvian coast and San Juan de Marcona, respectively. In the same areas, Burmeister's porpoise (n=67) fed on anchovies (90.37%, 81.89%), *O. regia* (6.64%, 0%), *Anchoa* sp. (1.13%, 0%), *N. crockery* (0%, 8.53%) and *M. gayi* (0.65%, 8.4%). Bottlenose dolphins (n=22) consumed *L. parvicauda* (39.24%), *Sphiraena* sp. (13.48%), *S. sagax* (13.31%), *Prionotus* sp. (9.59%), *M. gayi* (7.43%), *T. picturatus* (4.41%) and *E. ringens* (4.06%). The use of the Shannon & Wiener, Levins and Czekanowski's indexes in combination with the feeding patterns of the sampled species indicated an opportunistic feeding strategy with respect to their preys. The four cetacean species studied are predators of both pelagic and mesopelagic large schooling fish species, and demonstrate no selectivity towards prey species but towards social behaviour and habitat. An average linkage cluster analysis showed high levels of similarity in the diets of the studied cetaceans. This low diversification and a high degree of overlap in trophic niches is probably related to the high productivity of the Peruvian upwelling ecosystem.

KEY WORDS: LONG-BEAKED COMMON DOLPHIN; DUSKY DOLPHIN; BURMEISTER'S PORPOISE; BOTTLENOSE DOLPHIN; HABITAT; FEEDING ECOLOGY; COMPETITION

INTRODUCTION

The Peruvian Sea is one of the most productive ecosystems in the world (Ryther, 1969), both biological and economic, supporting a great variety of fisheries that provide food for humans and prime material for industry. Despite its exploitation, our knowledge of the trophic relationships of this ecosystem is very basic, mainly that concerned with the Peruvian anchovy *Engraulis ringens* and its predators (Pauly and Tsukayama, 1987). However, the study of trophic relations among top predators of a marine ecosystem is useful for the rational management of its populations. Maintaining a productive marine ecosystem requires responsive fisheries policies and administration, and the implementation of legal measures for the long-term conservation of the marine environment.

The Peruvian anchovy is the most exploited fishery resource in Peru, and is the biological resource that has produced the greatest income of foreign currency for the Peruvian State for several decades. The over-exploitation of anchovy in the early 1970's, in combination with El Niño, produced the collapse of its populations and its fishery, and its effects are experienced even now (Jordan, 1982). Together with the anchovy its predators also collapsed, such as the conspicuous case of guano birds whose populations declined dramatically (Duffy *et al*., 1984). However, the effects of the anchovy collapse on Peruvian small cetaceans, among the most important predators of the Peruvian Current system, were not studied at that time, partly due to the lack of trained scientists.

Studies of the exploitation of cetaceans in Peru by artisanal and industrial fisheries started late 1984 by scientists of the Peruvian Centre for Cetacean Research (CEPEC) and associates (e.g. Read *et al.,* 1988; Van Waerebeek and Reyes, 1990; García-Godos, 1993; Van Waerebeek *et al*., 1994a,b). Of the 31 cetacean species recorded to date in Peruvian waters (García-Godos and Van Waerebeek, 1994), this exploitation is concentrated mainly on four species of small cetaceans: the dusky dolphin *Lagenorhynchus obscurus*, the long-beaked common dolphin *Delphinus capensis*, the bottlenose dolphin *Tursiops truncatus* and the Burmeister's porpoise *Phocoena spinipinnis*. Despite massive exploitation in the late 1980's and early 1990's, before it was permanently banned for being unsustainable, there was only a fragmentary knowledge of the natural history of these species. Pauly and Tsukayama (1987) recognized the almost total lack of knowledge of the diet of small cetaceans as a limiting factor for designing a model for the management of fisheries in the Peruvian-Chilean region.

Few papers have documented the diet of small cetaceans in the Southeast Pacific, and none addressed the food of small cetaceans as a community of predators. Van Waerebeek *et al.* (1990) found anchovy, cachema (*Cynoscion analis*), Pacific Pilchard (*Sardinops sagax*) and squids as the main food of coastal bottlenose dolphin, while the offshore population feeds on lanternfish, pilchard and mackerel. McKinnon (1994), studying the diet of the dusky dolphin, found anchovy and mackerel (*Trachurus picturatus*) as the main food of this species. Reyes and Van Waerebeek (1995) report anchovy as the main prey of Burmeister's porpoise. There is no information on the food of long-beaked common dolphin. Here we present a comprehensive study of the diet of *D. capensis* in comparison with that of the three other main small cetacean species of the Peruvian Current ecosystem. We search for differences and similarities in their diets with the aim of defining their respective ecological roles.

METHODOLOGY

Sample

A total of 281 stomach contents of small cetaceans were examined for the purpose of this study, which were taken from cetaceans landed by artisanal fisheries in the ports of Ancón, Pucusana, Cerro Azul and San Juan de Marcona (SJ Marcona). The samples were collected by the authors between 1987 and 1993. The sample consists of stomach contents of long-beaked common dolphin (n=117), dusky dolphin (n=73), bottlenose dolphin (n=22) and Burmeister's porpoise (n=69). To allow comparison with McKinnon (1994), the samples collected in the ports of Pucusana, Cerro Azul and Ancón were grouped as from single stocks named 'central coast of Peru', because all are situated within a coastal strip of ca. 160km long (Fig. 1). Reason for doing so is that the marine ecosystem of the central coast of Peru is practically homogeneous (Brainard and McLain, 1987; Peña *et al*., 1989). Dusky dolphin and Burmeister's porpoise specimens were also sampled at San Juan de Marcona. The sample distribution is shown in Table 1.

Samples were collected in the field, at respective fish markets. Stomachs (fore, main and pyloric) of freshly landed cetaceans were dissected and its contents was sieved and washed over plastic recipients. Hard items such as otoliths, squid beaks and others were recovered from the recipient. Otoliths were stored dried; squid beaks kept in 70% ethanol. All material and field data are deposited at the *Museo de los Delfines*, CEPEC, Pucusana. Otoliths were identified by the first author, following the morphological patterns described by García-Godos (2001) and reference collections. Squid beaks were grouped as cephalopods and for the time being not further identified.

Data analysis

Main food parameters studied included the 'frequency of occurrence' (FO), presented as a percentage, and the 'prey percentage of composition' (PC) for each species, as defined by Frost and Lowry (1980):

Frequency of Occurrence (FO):

$$FO = 100 \times N_i / N \quad \text{, being}$$

N_i = Number of stomach contents where the prey species *i* is present
N = Total number of stomach contents examined

Prey Percentage of Composition (PC):

$$PC = 100 \times T_i / T \quad \text{, being}$$

T_i= Number of individuals of the prey species *i*
T= Total of individuals preys in the whole sample

The number of individuals found is the minimum number of preys recovered in the stomach contents, that is, the number of *sagittae* otoliths divided by two (Frost and Lowry, 1980; McKinnon, 1994).
With the purpose of verifying differences in the diet with respect to reproductive status the sample was divided into five categories: 1) immature females, 2) resting adult females, 3) reproductive females (pregnant or lactating), 4) immature males and 5) adult males. Reproductive status was determined in the field in agreement with the macroscopic examination of gonads and other reproductive organs as described in Van Waerebeek and Read (1994).

To determine differences in the mean percentage of prey consumption, among seasons, reproductive statuses and diversity (see below) non-parametric tests were used, including Kruskal-Wallis one-way analysis of variance by ranks (statistic is indicated by KW), Mann-Whitney (statistic is MW) and Chi– square tests (Siegel, 1956; Siegel and Castellan, 1988). Mann-Whitney test was also used to determine bias in the sample, probably caused by a more intensive sampling in 1987.

The trophic niche breadth was estimated for each species sampled using the Shannon and Wiener index of diversity (H), as defined by Krebs (1989):

$$H = \Sigma (p_i)(\log_2 p_i) \quad \text{, being}$$

H= Shannon and Wiener diversity index
p_i = ratio of individuals of prey species *i*

The logarithmic base of this index is 2, thereon its units are bits and its range is from zero to infinite. With the aim of a better interpretation of this index we use the standardized form of this index (Hstd), whose range is from zero to one (Krebs, 1989):

$$Hstd = H/\text{Log}_2 n \quad \text{, being}$$

H std = Standardized Shannon-Wiener diversity index
H= Shannon and Wiener diversity index
n = Total number of prey species

To determine the level of similarity in the diet of the small cetaceans studied we used the Simplified Morisita's index of similarity (Krebs, 1989):

$$C_H = 2 \Sigma p_{ij} p_{ik} / (\Sigma p^2_{ij} + \Sigma p^2_{ik}) \quad \text{, being}$$

C_H = Simplified Morisita's index of similarity between species *j* and *k*
p_{ij}, p_{ik} = ratio of the prey species *i*

For a graphical view of the diversification of the diet in the small cetacean community we run a mean linkage hierarchical cluster analysis (Krebs, 1989), using the Morisita's simplified similarity index and the general ratio of prey species for each cetacean species.
The overlapping level between the general consumption of small cetaceans and the landings of the pelagic industrial fishery was preliminarily determined using the last index. The data for fishery landings were taken from the statistics published by Ñiquen and Bouchon (1995).

Table 1. Distribution of the sample of stomach contents collected according to season (summer, SU; autumn A; winter, W; spring, S), year and sampling location (Ancon, A; Cerro Azul, CA; Pucusana, P; Marcona, M).

	SPECIES			
Season-year	*D. capensis*	*L. obscurus*	*P. spinipinnis*	*T. truncatus*
SU-87	7P	13P	3P	7P
A-87	6P		2P	
W-87	36P	10P	11P	
S-87	17P	4P	9P	1CA
SU-88			2P	4P
A-88	7P		11P	
W-88	2P		1P	
S-88				
A-89			1P	4P
W-89	1P		1P	1P
S-89				3P
SU-90		13P, 7CA		
A-90				1P
W-90	1P			
SU-91	1P, 8A	3 A	9 A	
W-91	21A			
SU-92			1 A	1A
S-92		20M	14 M	
SU-93	2CA	3 M	3 M	
A-93	3CA			
W-93	5CA			
TOTAL	117	73	69	22

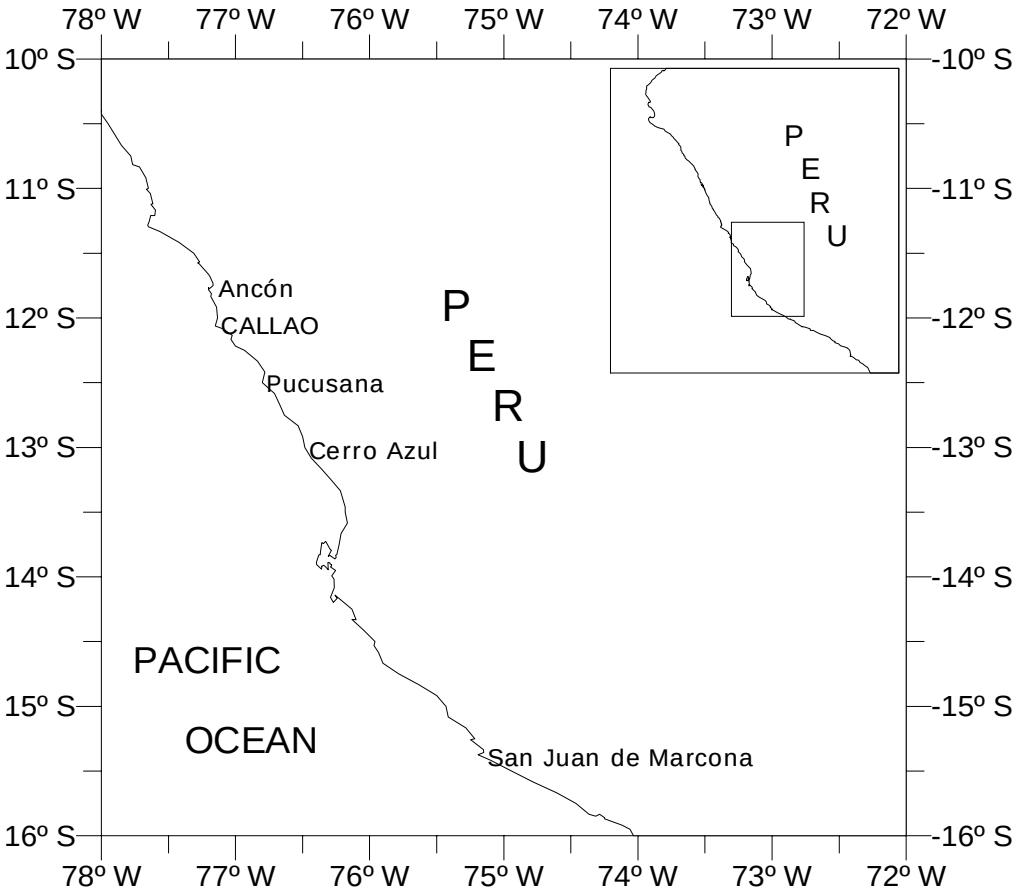

Fig. 1. Sampling locations along the Peruvian coast

Table 2. Presence (X) of prey species in the diet of four species of small cetaceans in Peru (ND= bony fish species recognized as different but not identified to species level).

	D. capensis	*L. obscurus*	*T. truncatus*	*P. spinipinnis*
Engraulis ringens	X	X	X	X
Odontesthes regia	X	X	X	X
Merluccius gayi	X	X	X	X
Sardinops sagax	X	X	X	X
Seriolella violacea	X			X
Trachurus picturatus	X	X	X	
Prionotus sp.	X	X	X	
Anchoa nasus	X			X
Scomber japonicus	X	X	X	
Scomberesox saurus	X		X	X
Vincigerria lucetia	X	X		
Mictophum nitidulum	X	X		
Lampanyctus parvicauda	X	X	X	
Sphyraena sp.	X	X	X	
Normanichthys crockeri	X	X		X
Aphos porosus	X	X		
Ophicthius pacifici	X			X
Mugil cephalus		X	X	
Cheilopogon heterurus		X		
Stellifer minor			X	
Galeichthys peruanus			X	
Labrisomus philippii			X	
Sciaena deliciosa				X
Euphasia sp.	X			
Pleuroncodes monodon	X			
Cephalopoda	X	X		X
ND 1	X		X	X
ND 2	X		X	
ND 3		X		
ND 4	X			
ND 6		X		
ND 8		X		
ND 9		X	X	
ND 10			X	
ND 11			X	
ND 12			X	
ND 13		X		
ND 14			X	
ND 15			X	
ND 16				X
ND 17	X			

Table 3. Percentage of composition of fish preys of long-beaked common dolphins caught off the central coast of Peru.

LOCATION	SEASON	n	*Engraulis*	*Odontesth*	*Merluccius*	*Sardinops*	*Seriolella*	*Trachurus*	*Scomber*	*Prionotus*	*Anchoa*	*Scomber*	*Vincigerri*	*Mictophur*	*Lampany*	*Sphyrna*	*Normanic*	*Aphos*	*Ophichthi*	ND 1	ND 2	ND 3
Pucusana	Summer 1987	7	89.94	1.28			2.14	6.21				0.21		0.21								
Pucusana	Autum1987	6	18.18		1.07	1.60		4.81					6.42	8.56	59.36					1.07		
Pucusana	Winter 1987	36	96.36	0.68	0.17	1.16	0.06	0.7	0.14	0.62	0.11			0.03					0.03			
Pucusana	Spring 1987	17	43.16		0.11	0.07		1.03				1.24	26.64	8.35	19.31	0.11	0.04			0.28	0.04	0.67
Pucusana	Autum 1988	8	95.68	0.22		3.24		0.43		0.43												
Pucusana	Winter 1988	2	100																			
Pucusana	Winter 1989	1	94.79					4.17	1.04													
Pucusana	Winter 1990	1	25.93					74.07														
Pucusana	Summer 1991	1	3.19	51.48	42.14	3.19																
Ancon	Summer 1991	8	36.21	62.93	0.86																	
Ancon	Winter 1991	21	87.46	0.19	12.14	0.19																
Cerro Azul	Summer 1993	1	32.12		67.88																	
Cerro Azul	Autum 1993	3	60	7.86		0.71				14.29							11.43	5.71				
Cerro Azul	Winter 1993	5	100																			
GENERAL		**117**	**71.14**	**3.54**	**4.49**	**0.8**	**0.12**	**1.42**	**0.06**	**0.45**	**0.04**	**0.37**	**7.89**	**2.62**	**6.77**	**0.03**	**0.18**	**0.08**	**0.01**	**0.1**	**0.01**	**0.2**

Table 4. Frequency of occurrence (FO) of preys of long-beaked common dolphins caught off the central coast of Peru.

	Engraulis	*Odontesth*	*Merluccius*	*Sardinops*	*Seriolella*	*Trachurus*	*Scomber*	*Prionotus*	*Anchoa*	*Scombere*	*Vincigerri*	*Mictophun*	*Lampanyc*	*Sphyrna*	*Normanic*	*Aphos*	*Ophichthi*	ND 1	ND 2	ND 3	Eufausids	Crustacea	Squids
FO	97	21	17	19	2	19	2	8	1	7	9	11	9	1	3	1	1	3	1	2	2	9	14
%FO	82.91	17.95	14.53	16.24	1.71	16.24	1.71	6.84	0.85	5.98	7.69	9.40	7.69	0.85	2.56	0.85	0.85	2.56	0.85	1.71	1.71	7.69	11.97

RESULTS

Long-beaked common dolphin

The food of long-beaked common dolphins was mainly fish, comprising 98.71% of preys (9,828 individuals), while the remainder was composed of squids and crustaceans. From the 20 fish prey species observed, six were present at least in 10% of the pooled sample. The Peruvian anchovy *Engraulis ringens* was the most frequently consumed prey (81.51% of occurrence), followed by silversides *Odontesthes regia* (17.65%), Peruvian pilchard *Sardinops sagax* (15.97%), mackerel *Trachurus picturatus* (15.97%), hake *Merluccius gayi* (14.29%) and squids (11.76%). By number, the Peruvian anchovy was the most important prey (71.14%), followed by the Panama's lightfish *Vincigerria lucetia* (7.89%), and the slimtailed lanternfish *Lampanictus parvicauda* (6.77%). Other preys included hake (4.49%), Peruvian silverside (3.54%), nitti lanternfish *Mictophum nitidulum* (2.62%) and mackerel (1.42%). Tables 2, 3 and 4 summarize the diet of *D. capensis.*

No statistic difference was found in prey composition between 1987 and the whole period sampled (U-Mann-Witney= 185.00, P>0.6). Significant differences were found in the mean consumption of anchovy (KW= 14.042, P<0.05, df = 6) and silversides (KW= 24.498, P<0.01, df= 6) among seven sampling periods. For 1987, differences were found among seasons for anchovy (KW= 9.541, P<0.05, df= 3), slimtailed lanternfish (KW= 17.86, P<0.001, f.d.= 3), nitti lampfish (KW= 13.23, P<0.01, df= 3) and Panama's lightfish (KW= 18.416, P<0.001, df= 3). The largest amount of anchovy consumed in 1987 was during summer and winter, while meso-pelagic fishes named above had higher consumption during autumn and spring of that year (Table. 3).

Among reproductive status, no statistic differences were found either in the mean number of prey species (KW= 2.469, P=0.65, df= 4) nor in the number of preys consumed (KW= 2.021, P>0.7, df= 4) nor mean percentage of anchovy (KW= 4.527, P>0.3, df= 4). The body size of dolphins was significantly and positively related to the number of prey species (r=0.243, n=84, P<0.05) and the number of preys (r=0.283, n=84, P<0.01).

The standardized Shannon-Wiener index of diversity (H_{std}) obtained for the pooled sample was 0.394 (mean= 0.231, S.D.= 0.139). No statistic differences in the diversity of the diet were found among sampling periods (χ^2=7,600, P>0.8, 13 df, using Hmax as expected value). Increasing of the diversity of the diet was observed when different preys rather than anchovy dominated the diet. During spring 1987, when mesopelagic fish dominated the diet, H_{std} was 0.473, and during Autumn 1993, the diet dominated by mote sculpins had a standardized diversity of 0.411 (χ^2= 9.952, P>0.5, df=13) (Table 5).

Table 5. Diversity indexes of the diet of long-beaked common dolphins landed in Peru

PORT	DATE	H	H Std
PUCUSANA	Summer-87	0.624	0.144
PUCUSANA	Autumn-87	1.898	0.439
PUCUSANA	Winter-87	0.324	0.075
PUCUSANA	Spring-87	2.044	0.473
PUCUSANA	Autumn-88	0.308	0.071
PUCUSANA	Winter-88	0	0
PUCUSANA	Winter-89	0.333	0.077
PUCUSANA	Winter-90	0.826	0.191
PUCUSANA	Summer-91	1.336	0.309
ANCON	Summer-91	1.010	0.234
ANCON	Winter-91	0.573	0.133
CERRO AZUL	Summer-93	0.906	0.210
CERRO AZUL	Autum-93	1.776	0.411
CERRO AZUL	Winter-93	0	0
GENERAL		**1.701**	**0.394**
	Mean	0.854	0.231
	S.D.	0.658	0.139

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Table 6. Percentage of composition of fish preys of dusky dolphins caught off Peru.

LOCATION	SEASON	n	*Engraulis*	*Odontesth*	*Merluccius*	*Sardinops*	*Trachurus*	*Scomber*	*Prionotus*	*Vincigerria*	*Mictophun*	*Lampanyc*	*Sphyrna*	*Normanic*	*Aphos*	*Mugil*	*Cheilodac*	ND 1	ND 3	ND 4	ND 6	ND 8	ND 9	ND 13
Pucusana	Summer 1987	13	45.21				54.79																	
Pucusana	Winter 1987	10	93.66	0.47	0.47		5.4																	
Pucusana	Spring 1987	4	47.14			2.2	48.46	0.44				0.44					1.32							
Pucusana	Summer 1990	13	63.33	9.05		20	5.24					0.95	0.48			0.48							0.48	
Cerro Azul	Summer 1990	7	12.33	0.17		0.51		0.17		10.81	2.87	71.96	1.01					0.17						
Ancon	Summer 1991	3	94.74	3.51	1.75																			
Central Coast		**50**	**49.75**	**1.32**	**0.17**	**2.75**	**17.08**	**0.11**		**0.04**	**0.94**	**23.64**	**0.39**			**0.06**	**0.17**	**0.06**					**0.06**	
San Juan	Summer 1992	20	15.85		0.98			0.03	0.03	0.01		0.08		77.36	0.02				5.04	0.37	0.07	0.05	0.02	0.03
San Juan	Spring 1993	3	100																					
San Juan		**23**	**16.88**		**0.97**			**0.03**	**0.03**			**0.08**		**76.42**	**0.02**				**4.98**	**0.37**	**0.07**	**0.05**	**0.02**	**0.03**
GENERAL		**73**	**24.55**	**0.31**	**0.78**	**0.64**	**3.98**	**0.05**	**0.03**	**0.01**	**0.22**	**5.58**	**0.09**	**58.59**	**0.01**	**0.01**	**0.04**	**0.01**	**3.82**	**0.28**	**0.05**	**0.04**	**0.03**	**0.03**

Table 7. Frequency of occurrence (FO) of preys of dusky dolphins caught off Peru.

		Engraulis	*Odontesth*	*Merluccius*	*Sardinops*	*Trachurus*	*Scomber*	*Prionotus*	*Vincigerria*	*Mictophun*	*Lampanyc*	*Sphyrna*	*Normanic*	*Aphos*	*Mugil*	*Cheilodac*	ND 1	ND 3	ND 4	ND 6	ND 8	ND 9	ND 13	Squids
Central Coast	FO	35	8	3	10	28	2		1	1	6	2			1	2	1					1		2
	% FO	70.00	16.00	6.00	20.00	56.00	4.00		2.00	2.00	12.00	4.00			2.00	4.00	2.00					2.00		4.00
S.J. Marcona	FO	22		10			1	2	1		1		14	1				8	1	1	1	1	1	10
	% FO	95.65		43.48			4.35	8.70	4.35		4.35		60.87	4.35				34.78	4.35	4.35	4.35	4.35	4.35	43.48

Dusky dolphin

The diet of the dusky dolphin in the central coast of Peru was composed almost exclusively of fish, with 14 prey species and 1,815 individuals eaten, the remainder (0,01%) were squids. Anchovy was the most common (PC) prey consumed (49,75%), followed by the slimtail lanternfish (23,64%), mackerel (17,08%), and Panama's ligthfish (3,53%), among other species. Anchovy was also the most frequent prey species, being present in 71.43% of the stomach contents, with mackerel in the second place (57.14%), followed by pilchard (20.41%), silverside (16.33%) and slimtail lanternfish (12.24%). Dusky dolphins landed at S.J. Marcona ate mainly fish, with some squids present. There were 14 prey species recorded, accounting for 5,966 individuals. The mote sculpin *Normanichtys crockeri* was the main prey species consumed (76.42%), followed by the anchovy (16.88%) and an unidentified fish species (4.98%). However, the anchovy was the most frequent species consumed, with a frequency of occurrence of 95.65%, followed by the Mote sculpin (60.87%) and hake (43.48%). Tables 2, 6 and 7 summarize the diet of dusky dolphins..

There were no statistic difference between the percentage of preys consumed in 1987 and the rest of samples collected (U-Mann-Whitney= 64.00, P>0.1), therefore all the samples were pooled for further analysis. For the Peruvian central coast no difference was found in the mean consumption of anchovy (KW = 7.712, P>0,1, 4 df) among different sampling periods, with as important consumption of this prey in summer as in winter, but with some exceptions. Similarly, there were no differences in the main consumption of silverside (KW= 5.824, P>0.2, 4 df) nor slimtail lanternfish (KW= 6.968, P>0.1, 4 df). The mean consumption of mackerel showed significant differences (KW= 23.243, P<0.001, 4 df), because it was not present in the diet during two periods. For the samples collected in S.J. Marcona there were significant differences in the mean consumption of anchovy (U-Mann-Whitney= 51.00, P<0.05) and mote sculpin (U-Mann-Witney= 51.00, P<0.05) between spring 1992 and summer 1993, with both species as the most consumed prey by composition in each period, respectively.

No statistic differences were found in the central coast among reproductive statuses with respect to mean number of preys (KW= 6.287, P>0.1, 4 df) nor with respect to the mean number of species consumed (KW= 4.010, P>0.4, 4 df). Neither differences were found in the mean number of anchovy (KW= 2.452, P>0.6, 4 df) nor mackerel (KW= 6.869, P>0.1, 4 df) among reproductive statuses. No relationship existed between the number of prey species (r_s= 0.046, n= 42, P>0.7) and the number of individual fish consumed (r_s= 0.084, n= 42, P>0.6) with respect to the body size of the dolphin.

The standardized Shannon-Wiener index ($H_{std,}$, Table 8) of diversity obtained for the pooled sample of the Peruvian central coast was 0.5193 (mean = 0.261, SD= 0.125), while that obtained for S.J. Marcona was 0.284 (n= 2). No statistic differences in the diversity of the diet were found among sampling periods (χ^2= 1.174, P>0.9, 5 df) The combined diversity H_{std} for the two regions sampled was 0.408 (mean = 0.278, SD= 0.144).

Table 8. Diversity indexes of the diet of dusky dolphins landed in Peru

PORT	DATE	H	H Std
PUCUSANA	Summer-87	0.993	0.261
PUCUSANA	Winter-87	0.388	0.102
PUCUSANA	Spring-87	1.291	0.339
PUCUSANA	Summer-90	1.592	0.418
CERRO AZUL	Summer-90	1.360	0.357
ANCON	Summer-91	0.346	0.091
CENTRAL COAST		**1.977**	**0.519**
	Mean	0.995	0.261
	S.D.	0.477	0.125
S.J. MARCONA	Spring-92	1.060	**0.278**
S.J. MARCONA	Summer-93	0	0
S.J. MARCONA		**1.082**	**0.284**
GENERAL		**1.820**	**0.408**
	Mean	1.083	0.278
	S.D.	0.572	0.144

Table 9. Percentage of composition of fish preys of bottlenose dolphins caught off Peru.

LOCATION	SEASON	n	*Engraulis*	*Odontesth*	*Merluccius*	*Sardinops*	*Trachurus*	*Scombere*	*Scomber*	*Lampanyc*	*Sphyrna*	*Mugil*	*Prionotus*	*Stellifer*	*Galeichthy*	*Labrisomi*	ND 1	ND 2	ND 9	N 10	ND 11	ND 12	ND 14	ND 15
Pucusana	Summer 1987	7	0.93		21.05	15.17	6.19	0.93	0.62	18.27	30.96	0.31					4.33			1.24				
Pucusana	Summer 1988	4	3.57			3.57	33.93			44.64				7.14		1.79			1.79		3.57			
Pucusana	Autum 1989	4				41.99	5.19			4.76			48.05											
Pucusana	Winter 1989	1	100																					
Pucusana	Spring 1989	3				12.2				72.62	11.36													3.85
Pucusana	Autum 1990	1		2.44											97.56									
Ancon	Summer 1992	1			81.82					4.55									4.55			9.09		
Cerro Azul	Spring 1987	1																33.33					66.67	
GENERAL		22	4.06	0.09	7.43	13.31	4.41	0.26	0.17	39.24	13.48	0.09	9.59	0.35	3.46	0.09	1.21	0.09	0.17	0.35	0.17	0.17	0.17	1.64

Table 10. Frequency of occurrence (FO) of preys of bottlenose dolphins caught off Peru.

	Engraulis	*Odontesth*	*Merluccius*	*Sardinops*	*Trachurus*	*Scombere*	*Scomber*	*Lampanyc*	*Sphyrna*	*Mugil*	*Prionotus*	*Stellifer*	*Galeichthy*	*Labrisomi*	ND 1	ND 2	ND 9	N 10	ND 11	ND 12	ND 14	ND 15
FO	5	1	3	9	7	1	1	10	5	1	1	1	1	1	2	1	2	2	1	1	1	1
% FO	22.73	4.55	13.64	40.91	31.82	4.55	4.55	45.45	22.73	4.55	4.55	4.55	4.55	4.55	9.09	4.55	9.09	9.09	4.55	4.55	4.55	4.55

Bottlenose dolphin

The diet of bottlenose dolphins was composed of fish only, accounting for 1,157 fish individuals representing 22 prey species. The main prey species consisted of the slimtail lanternfish *Lampanyctus parvicauda* (39.24%), followed by the barracuda *Sphyraena* sp. (13.48%), the pilchard *Sardinops sagax* (13.31%) and the lumptail sarobin *Prionotus stephanophrys* (9.59%), among others species. Tables 2, 9 and 10 summarize the diet of bottlenose dolphins..

The slimtail lanternfish was the most frequently consumed species (45.45% FO), followed by pilchard (40.91% FO), mackerel (31.82%) and anchovy and barracuda, both with 22.73% FO, amongst other species.

There were no statistic differences in the percentage of preys consumed between 1987 and the rest of samples taken (U-Mann-Witney= 198.00, P=0.3), therefore all samples were pooled. There were no differences among sampling periods with respect to the mean number of slimtail lanternfish consumed (KW= 1.272, P>0.7, 3 df), anchovy (KW= 4.35, P>0.2, 3 df), pilchard (KW= 1.75, P>0.6, 3 df) and mackerel (KW= 1.87, P=0.6, 3 df).

There was no statistic differences with respect to reproductive statuses in the mean number of preys consumed (KW= 6.286, P>0.15, 4 df), nor in the number of preys eaten (KW= 3.527, P>0.4, 4 df). Neither were differences noted (Kruskall-Wallis Test, df = 4) in the mean consumption of slimtail lanternfish (P> 0.2), pilchard (P> 0.4), mackerel (P> 0.35) nor anchovy (P> 0.2) among reproductive statuses. No significant relationship was found between the size (standard body length) of the dolphin and the number of prey species consumed (r_s = 0.236, P>0.3, n= 18) and the number of individuals eaten (r_s =0.176, P>0.45, n=18).

The standardized Shannon-Wiener index of diversity ($H_{std,}$, Table 11) obtained for the pooled sample was 0.635 (mean= 0.297, S.D= 0.200). There were no statistic differences between sampling periods with respect to Shannon and Wiener indexes (χ^2=1.918, P> 0.95, 7df; with Hmax as the expected value: χ^2= 1.942, P>0.95, 7 df).

Table 11. Diversity indexes of the diet of bottlenose dolphins landed in Peruvian ports.

PORT	DATE	H	H_{Std}
PUCUSANA	Summer-87	2.578	0.578
PUCUSANA	Summer-88	2.043	0.458
PUCUSANA	Autumn-89	1.465	0.328
PUCUSANA	Winter-89	0	0
PUCUSANA	Spring-89	0.950	0.213
PUCUSANA	Autumn-90	0.165	0.037
ANCON	Summer-92	0.957	0.215
CERRO AZUL	Spring-87	0.918	0.206
GENERAL		**2.832**	**0.635**
	Mean	1.323	0.297
	S.D.	0.890	0.200

Burmeister's porpoise

In the central coast of Peru fish composed the diet of the Burmeister's porpoise almost exclusively (98.36%). Fish was represented by eight species which accounted for 1,070 individuals (Tables 2 and 12). Anchovy was the main prey (90.37%) followed by silverside (6.64%), among other species. Anchovy was present in 90.38% of stomach contents, followed by silverside (9.62%) and hake (7.38%).

In S.J. Marcona fish (96.8%) and squid composed the diet. Fish accounted for 762 individuals, representing eight species. Anchovy was the main food by number (81.89%), followed by the Mote sculpin (8.53%) and hake (8,40%). Anchovy was present in 76.47% of the sample, followed by squids (52.94%), hake (35.29%) and Mote sculpin (23.53%). Tables 2, 12 and 13 summarize the diet of Burmeister's porpoises..

There were no significant differences in the percentage of preys consumed in 1987 and the rest of samples of the central coast (U-Mann-Witney= 22.00, P>0,29), therefore all samples were pooled. There were no differences in the mean consumption of anchovy (KW= 9.798, P>0,10, df= 6) nor silversides (KW = 10.601, P>0,10, df= 6). There were no statistic differences (Mann-Witney test) in the consumption of anchovy (P> 0.4), hake (P>0.1), Mote sculpin (P>0.8) and squids (P>0.2) between spring 1992 and summer 1993 in S.J. Marcona.

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Table 12. Percentage of composition of fish preys of Burmeister's porpoises caught off Peru.

LOCATION	SEASON	n	*Engraulis*	*Odontesth*	*Merluccius*	*Sardinops*	*Trachurus*	*Anchoa*	*Sciaena*	*Scombere*	*Ophichthid*	*Normanic.*	ND1	ND 16
Pucusana	Summer 1987	4	95.00	5.00										
Pucusana	Autum1987	2	89.47		5.26		5.26							
Pucusana	Winter 1987	11	98.22		0.59		0.59	0.59						
Pucusana	Spring 1987	9	97.95		1.37				0.68					
Pucusana	Summer 1988	2	61.22	37.41		1.36								
Pucusana	Autum 1988	11	96.48	1.41			0.35		1.41	0.35				
Pucusana	Winter 1988	1	100.00											
Pucusana	Autum 1989	1	100.00											
Pucusana	Winter 1989	1	100.00											
Ancon	Summer 1991	9	58.33	41.67										
Cerro Azul	Summer 1992	1	31.25					68.75						
Central Coast		**52**	**90.37**	**6.64**	**0.65**	**0.19**	**0.37**	**1.12**	**0.56**	**0.09**				
SJ Marcona	Summer 1993	13	75.39		14.32	0.45			0.45		0.22	8.72	0.22	0.22
SJ Marcona	Autum 1993	4	91.11						0.63			8.25		
San Juan Marcona		**17**	**81.89**		**8.40**	**0.26**			**0.52**		**0.13**	**8.53**	**0.13**	**0.13**
GENERAL		**69**	**86.84**	**3.88**	**3.88**	**0.22**	**0.22**	**0.66**	**0.55**	**0.05**	**0.05**	**3.55**	**0.05**	**0.05**

Table 13. Frequency of occurrence (FO) of preys of Burmeister's porpoises caught off Peru.

		Engraulis	*Odontesth*	*Merluccius*	*Sardinops*	*Trachurus*	*Anchoa*	*Sciaena*	*Scombere*	*Ophichthid*	*Normanic.*	ND1	ND 16	Squids
Central Coast	FO	47	5	4	1	3	2	3	1					4
	% FO	90.38	9.62	7.69	1.92	5.77	3.85	5.77	1.92					7.69
SJ Marcona	FO	13		6	1			2		1	4	1	1	9
	% FO	76.47		35.29	5.88			11.76		5.88	23.53	5.88	5.88	52.94

There were no differences among reproductive statuses with respect to the mean number of preys (KW= 6.526, P>0.15, 4 df) nor the mean number of prey species consumed (KW= 7.229, P>0.1, 4 df). There were no differences among reproductive statuses with respect to mean number of anchovy (KW= 5.281, P>0.2, 4 df) nor the mean percentage of anchovy consumed (KW= 3.697, P>0.4, 4 df). We found a significant relationship between the number of preys consumed (r_s =0.41, P=0.01, n=46) and the porpoise's size, but there were no relation with the number of prey species consumed (r_s =0.03, P>0.8, n=46).

The standardized Shannon-Wiener index (H_{std}, Table 14) of diversity obtained for the pooled sample of the Peruvian central coast was 0.203 (mean= 0.133, SD= 0.129, n= 11), while that obtained for S.J. Marcona was a higher 0.313 (n=2). There were no differences in the Shannon-Wiener indexes calculated for every period sampled (x^2=3.501, P>0.95, 10 df; with Hmax as the expected value: x^2= 1.699, P>0.99, 10 df).

Table 14. Diversity indexes of the diet of Burmeister's porpoises landed in Peru.

PORT	DATE	H	H Std
PUCUSANA	Summer-87	0.286	0.095
PUCUSANA	Autumn-87	0.591	0.197
PUCUSANA	Winter-87	0.157	0.052
PUCUSANA	Spring-87	0.163	0.054
PUCUSANA	Summer-88	1.048	0.349
PUCUSANA	Autumn-88	0.281	0.094
PUCUSANA	Winter-88	0	0
PUCUSANA	Autumn-89	0	0
PUCUSANA	Winter-89	0	0
ANCON	Summer-91	0.980	0.327
CERRO AZUL	Summer-92	0.896	0.299
CENTRAL		**0.610**	**0.203**
	Mean	0.400	0.133
	S.D.	0.389	0.130
S.J. MARCONA	Spring-92	1.145	0.382
S.J. MARCONA	Summer-93	0.466	0.294
S.J. MARCONA		**0.939**	**0.313**
GENERAL		**0.862**	**0.240**
	Mean	0.462	0.165
	S.D.	0.409	0.141

Inter-specific relations

The mean linkage cluster analysis applied to the ratio of contribution of the prey species to the pooled sample of each cetacean studied, using as similarity measure the simplified Morisita's index (FIG.XXXX) shows that the diet of the four small cetaceans species is very similar, with overlapping trophic niches. The closer species are the Burmeister's porpoise and the Long-beaked common dolphin, with a similarity of 0.965. This cluster joins with the dusky dolphin at a similarity of 0.920. The bottlenose dolphin joins this cluster at a similarity level of 0.873. Table 14 shows the similarity matrix calculated for this analysis.

The similarity matrix calculated for 1987 among *D. capensis*, *L. obscurus* and *P. spinipinnis* did not differ greatly from that obtained for the pooled samples. This result supports the methodology used for the pooled data.

High similarity values were found between the general diet of small cetaceans and the industrial fishery of pelagic resources (Ñiquen and Bouchon 1995), at a level of 0.915 (simplified Morisita's index). This high similarity was because the main fishery resource for the Peruvian industry is anchovy, the main prey of small cetaceans.

Table 15. Similarity matrix of the diet of small cetaceans of the central coast of Peru.

Simplified Morisita's index				
	D. capensis	*L. obscurus*	*T. truncatus*	*P. spinipinnis*
D.capensis	1	0.875	0.165	0.965
L.obscurus		1	0.460	0.780
T. truncatus			1	0.074
P.spinipinnis				1

Simplified Morisita's index, 1987			
	D. capensis	*L. obscurus*	*P. spinipinnis*
D.capensis	1	0.896	0.944
L.obscurus		1	0.877
P.spinipinnis			1

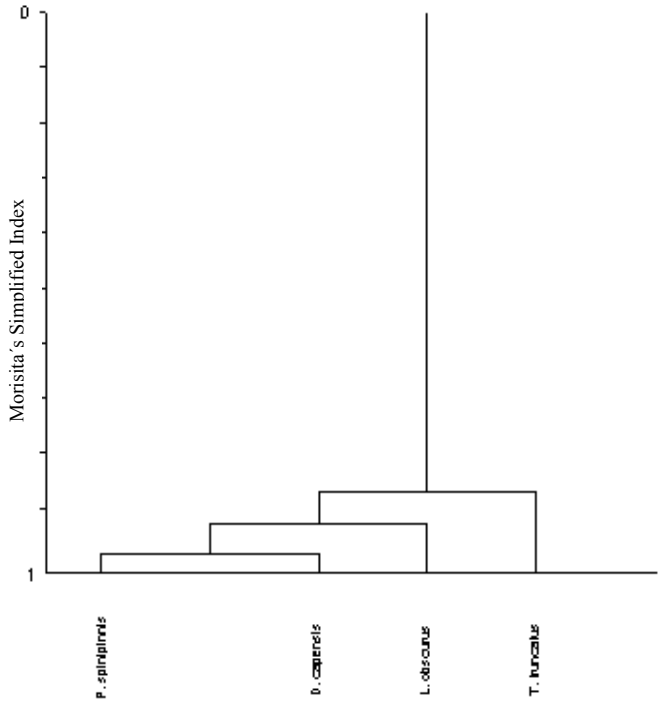

Figure 2. Mean linkage cluster analysis of the diet of four species of small cetaceans from the Peruvian central coast

DISCUSSION

Long-beaked common dolphin

Sekigushi *et al*. (1992) found that squids, Cape anchovy *Engraulis capensis*, pilchard *Sardinops ocellatus* and mackerel *Trachurus trachurus* were the main preys of common dolphins in South Africa. Later, Young and Cockcroft (1994) found pilchard and myctophids in its diet in the same area, and concluded that the common dolphin is an opportunistic feeder. In California, Heynin and Perrin (1994) reported a similar rate of anchovy and hake in the stomachs of *D. capensis*.

In this study, fish species closely related to preys found in the other ocean provinces were the main food, while cephalopods constituted a minor part of the diet. In the Peruvian Sea the anchovy is the key fish species and is the main food of such top predators as the 'guano birds' (guanay cormorants *Phalacrocorax bougainvillii*, Peruvian boobies *Sula variegata* and Peruvian pelicans *Pelecanus thagus*) (Jahncke and Goya, 1997) and pinnipeds, i.e. the South American fur seals *Arctocephalus australis* and the South American sea lion *Otaria flavescens* (Vásquez, 1995). Among Peruvian cetaceans, McKinnon (1994) reported the dusky dolphin as consumer of anchovy. Moreover, the Peruvian anchovy on its own maintains a huge industrial fishery, the biggest in the world, due to its extraordinary abundance and the high productivity of the Peruvian current ecosystem (Pauly and Tsukayama, 1987).

The anchovy and silverside occurrence in the diet of long-beaked common dolphins indicates a pelagic feeding strategy, however with an important neritic component, which could be named offshore-neritic. Indeed, long-beaked common dolphins seem to be largely limited to waters above the continental shelf (CEPEC, unpublished data). The results shown in the present study agree with those found in South Africa and California. Sekiguchi *et al*. (1992) indicate that long-beaked common dolphins feed on both shallow water and deep-water fish, and closer to the coast and over the shelf than other cetaceans off South Africa. Norris and Prescott (1961) and Fitch and Brownell (1968) reported a similar feeding behavior in coastal waters off California.

This study suggest that Peruvian long-beaked common dolphins forage mainly in pelagic waters on the shelf, feed on anchovy and other fish species near the surface, and dive for mesopelagic preys at least to 200m depth, as suggested by mesopelagic fish found in 1987. However, the occurrence of the latter could be influenced by the presence of warm water currents as a consequence of El Niño or other warming events (Arntz and Fahrbach, 1996).

Although the anchovy was the main prey species overall, it was not the first prey during all the sampled periods, suggesting that *D. capensis* has some adaptability to feed on other preys, despite the high availability of anchovy. The occurrence of Panama's lightfish and myctophids only during El Niño 1987 (Table 3), and mote sculpin during autumn 1993, suggests an opportunistic feeding behaviour related to local availability of food. Wisnar (1976) recorded *L. parvicauda*, a warm-water mesopelagic species, very close to shore in central Peru, while the mote sculpin, a species from sub-antarctic waters, was reported in the fishery since 1991 (Bouchon and Quiroz, 1996; Quiroz *et al*., 1996). The temporal availability of these preys seems to be opportunistically exploited by long-beaked common dolphins, explaining the important, but temporal, contribution to their diet.

Peruvian *D. capensis* seem to depend on pelagic and mesopelagic prey, mainly large schooling fish species such as anchovy, mycthophids, mote sculpin and hake. Also in this sense, long-beaked common dolphins forage opportunistically on available prey species, but selectively on their social behaviour, preferring schooling fish. The Shannon-Wiener indexes show a low diversity value, indicating a narrow trophic niche breadth, which may be explained by the high availability of anchovy in the sampled area, which is permanent and abundant (Pauly and Tsukayama, 1987) leading to the default prey of *D. capensis* in Peru.

Opportunistic feeding behaviour appears to be characteristic of common dolphins. On the southeast coast of South Africa long-beaked common dolphins feed on the more available preys and its diet is an indicator of the abundance of local resources (Young and Cockcroft, 1994). Klinowska (1981) indicates that common dolphins are opportunistic feeders and that their stomach contents reflect the local offer. Similar results were obtained by Collet (1981). Moreover, Sekigushi *et al*. (1992) report that common dolphins feed on pelagic fishes, apparently without any kind of selectivity and can be an indicator of these resources in time and space, in agreement with Gaskin (1982).

The preys of long-beaked common dolphin were pelagic (anchovy, silverside, mote sculpin) and meso-pelagic fish (lanternfish and lightfish), that aggregate in large schools, and demersal fish like hake, which also forms pelagic schools (Mejía and Jordán 1979). Off Peru's central coast anchovy schools are found between the surface and 30m depth at night, while during daylight they are found at 30-60m depth; however, anchovy is found near the surface only when attacked by predators (Jordán and Vildoso, 1965). In contrast, lanternfish and lightfish are mesopelagic species with huge diel migrations, from surface waters at night down to 1,000m during the day (Robinson and Craddock, 1983; Wisnar, 1976). *Lampanyctus parvicauda* is found mainly at 400m depth during the day and migrates to 200m at night (Fitch and Brownell 1968), although it has been collected at surface during the night (Wisnar 1976). The Panama's lightfish live at depths of 200-300m at day and at surface during the night (Fitch and Brownell, 1968).

There is no information about abundance and distribution of lanternfish and lightfish for years sampled in the present study. Fitch and Brownell (1968), indicated that common dolphins off California feed between 200 and 250 meters depth, near to the bottom. Gaskin (1982) suggested that common dolphins make deep dives for food at night and during the day stay near the surface. Sekigushi *et al.* (1995) showed experimentally that common dolphins from South Africa mainly feed between late night and early day. In Peruvian waters nothing is known about foraging habits of common dolphins, which underscores the need of research.

Our results do not permit to suggest seasonality in diet, mainly because the anchovy consumption decreased with the rise of alternative preys as different as mycthophids, silversides, mackerel and hake. However, the greater

consumption of anchovy occurred during winter, when anchovy disperses and deeps, and summer, when it concentrates inshore (Jordán and Vildoso, 1965; Jordán, 1982).
Young and Cockroft (1994) found differences between sexes, size, and reproductive status in the diet of common dolphins of South Africa. Adult females showed a more diverse diet than males, and they associated it with nursery groups. However, such differences were not found in the present study, possibly because of sampling discontinuity.

Dusky dolphin
The diet of the dusky dolphin was mainly composed of schooling pelagic fish (anchovy, mote sculpin and mackerel) and mesopelagic fish (slimtail lanternfish and Panama's lightfish), with an important incidence of neritic fish, such as silverside. On the Atlantic coast of South America, Würsig and Würsig (1980), Crespo *et al*. (1994) and Koen *et al.* (1998) also recorded anchovy (*Engraulis anchoita*) as the main prey of dusky dolphins off Argentina. Sekiguchi *et al*. (1992) reported that South African dusky dolphins feed in areas closer to shore and on the shelf than other cetacean species, including both pelagic and deep water prey species, as was found in Peru.

The habitat of the main prey species suggests that Peruvian dusky dolphins feed mainly in the pelagic layer, from the surface to 60 meters deep, with occasioinal deeper dives, up to 200m, in search of mesopelagic and demersal preys. Sekigushi *et al*. (1995) showed experimentally that dusky dolphins off South Africa feed at any time of the day without any temporal pattern. Off Argentina dusky dolphins forage at day, mainly in the afternoon (Würsig and Würsig, 1980). There is no observational information on dive depths in Peru.

McKinnon (1994) recorded 92.5% by weight of anchovy in the diet of dusky dolphins sampled between 1985 and 1986. Other fish reported were mackerel, hake and pilchard, but no mesopelagic species, which suggest changes in the food supply, or in feeding habits, since the mid-1980s. Sekiguchi *et al*. (1992) found South African dusky dolphins to feed mainly on carangids (mackerel), hake and lanternfishes as well as deep-water squids, suggesting that they make deep dives at night.

The significant difference in anchovy consumption between Peru's central coast and south coast (S.J. Marcona), where it is largely replaced by mote sculpin, suggest low selectivity in the diet of Peruvian dusky dolphins. Mote sculpin is a species of sub-antarctic waters and has been reported in the area in important landings from 1991 (Bouchon and Quiroz, 1996; Quiroz *et al*., 1996). The southern limit of distribution of the Northern-Central stock of anchovy is situated at 14°S (Pauly and Tsukayama, 1987), i.e. near S.J. Marcona, where the anchovy becomes relatively scarce, despite the strong upwelling. Dusky dolphins then appear to have taken advantage of the high biomass of mote sculpin present during the sampling period, revealing an opportunistic foraging strategy.
McKinnon (1994) found a mean size of prey of 30cm with a mean mass of 300g, and the anchovy size consumed was smaller than those caught by the fishery, concluding that the dusky dolphin is an opportunistic feeder with respect to fish size.

Using the results by McKinnon (1994) for calculating a diversity index we found that the standardized Shannon-Wiener index (H_{std}) was 0.143, which was largely influenced by the great proportion of anchovy in the diet. The diversity index found in this paper shows a relatively wide trophic niche breadth for the central coast of Peru, while narrow for S.J. Marcona. The diversity of the diet thus seems influenced by differing food supplies in both areas. Off the central coast, anchovy was the main food item, in agreement with its usual abundance (Pauly and Tsukayama, 1987), constituting 50% of the diet by composition. Together with anchovy, other species composed the remainder 50% of the diet, resulting in a moderately wide niche breadth. On the other side, the availability of mote sculpin off southern Peru since 1991 and its high percentage in the diet of dusky dolphins sampled in S.J. Marcona (76%) resulted in a narrow niche breadth. We conclude that dusky dolphins do not depend on a single prey species, instead it would eat the more abundant and more available prey. The Peruvian dusky dolphin is a moderately opportunistic feeder with respect to prey species, but a specialist in terms of consuming schooling fish.

Bottlenose dolphin
The diet of the bottlenose dolphin in Peru consisted mainly of six prey species consumed with more than 10% in the frequency of occurrence. The main preys were mesopelagic fish, with high diel migration. The diet composition obtained from our sample agrees with that observed for the offshore ecotype of the bottlenose dolphin from Peruvian waters (Van Waerebeek *et al.*, 1990). The latter authors found anchovy and lanternfish to be the main prey of, respectively, coastal and offshore bottlenose dolphins.

Considering the bathymetric distribution of its main preys (Wisnar, 1976; Fitch and Brownell, 1968), the feeding of bottlenose dolphins in Peru occurred from the surface to at least 200m depth. The bathymetric distribution of feeding depends on the time of the day, because lanternfish have an evident diel migration (Wisnar, 1976) and it can be found at surface at night. Although coastal bottlenose dolphins commonly forage during the day near the surface (personal observations by authors), this cannot be affirmed for offshore bottlenose dolphins.

The values of the diversity indexes obtained for the diet of bottlenose dolphin are the highest obtained in this study, and allows us to consider this species as an opportunistic feeder with a wide trophic niche breadth. Cockcroft and Ross (1990) found that this species is also an opportunistic feeder off Natal, South Africa.

Burmeister's porpoise

Off Peru's central coast, the diet of the Burmeister's porpoise was based on a single species with more than 10% of the frequency of occurrence, and six species with more than 5%. Off southcentral Peru (S.J. Marcona) its food was based on five prey species most frequently consumed (10% FO). The main prey species was anchovy in both sampling areas, followed by silverside off the central coast and hake off south-central Peru. Lorna drum (*Sciaena deliciosa*) was present in both areas. Silverside and lorna drum are exclusively neritic species, while hake is demersal and its habits are not so close to shore (Mejía and Jordán 1979). Anchovy can be found in both neritic and pelagic waters (Reyes and Van Waerebeek, 1996). The Burmeister's porpoise is a neritic cetacean and its interactions with fisheries are close to shore (Read *et al.*, 1988; García-Godos, 1993; Reyes and Van Waerebeek, 1996; Van Waerebeek *et al*., 2002). A similar neritic behaviour has been observed for the harbour porpoise *Phocoena phocoena* (Rae, 1965, 1973), which predates on clupeids and gadids. On the base of its preys, near-shore sightings and reports of specimens captured in shore-seines, the Burmeister's porpoise occurs and would forage in the inshore-most neritic environments of all four cetacean species studied here. Despite this, the occurrence of mackerel includes a subtle offshore component or adaptability to occasional prey occurrence in its habitual environment.

Based on the distribution of anchovy (Jordán and Vildoso, 1965; Mejía and Jordán, 1979), we suggest that Burmeister's porpoise may dive to at least 80m depth in coastal waters. Rae (1973) indicated that harbour porpoise feeds on pelagic and mesopelagic fish, with a high amount of gadids. In Peru, and especially in S.J. Marcona, the diet contribution of gadids is smaller than those for harbour porpoises, and Burmeister's porpoise may have less of a demersal habit than its northern hemisphere relative.

The diversity indexes calculated appear to be small due to the high amount of anchovy observed in the diet of the Burmeister's porpoise. However, other prey species were consumed in important percentages during some periods (Table 14), and could be consumed as occasional resources in response to temporal availability. The consumption of silverside, hake, anchoa and mote sculpin, besides the anchovy, indicates that Burmeister's porpoise shows considerable adaptability with respect to food intake, although confined to schooling fish. The mean diversity indexes and the composition of the diet in periods with low anchovy lead us to define Burmeister's porpoise as a moderately opportunistic consumer.

Inter-specific relations

It was somewhat unexpected to find the long-beaked common dolphin and the Burmeister's porpoise share the first cluster, despite their relative taxonomic distance, and because long-beaked common dolphin is very often sighted in mixed schools with dusky dolphins (CEPEC, unpublished data). Even during fishery interactions both dolphins are captured together (García-Godos, 1993; Van Waerebeek and Reyes, 1994a,b). However, the diet of both species is still high, at 0.875. The bottlenose dolphin had the more distant diet from the species analyzed, because the sample belongs to the offshore ecotype.

Although the diets of the Burmeister's porpoise and the dusky dolphin are the closest of the central coast of Peru (simplified Morisitas' Index = 0.780) they are distant in S.J. Marcona (0.313). This difference could be a manifestation of different habitat distribution of both species. Dusky dolphin is a species of pelagic habits in coastal waters, while Burmeister's porpoise is a neritic species. Despite their different habits, they feed on anchovy and mote sculpin off S.J. Marcona, but probably on a different portion of its stock.

The high general similarity level found in the diet of the four species of small cetaceans studied could be interpreted in two ways. The similarity and diet overlap could cause a high degree of competition for food. However, if food availability is abundant enough, the four species of cetaceans may occur in trophic co-existence as seems to apply in the Peruvian sea due to the huge biomass of anchovy off Peru (Pauly and Tsukayama, 1987); food competition is absent when it is abundant (Giller, 1984).

The high similarity in the diet obtained would indicate a low level of diversification in their feeding habits, showing similar foraging strategies. This low diversification would be related to the vast availability of anchovy in the Peruvian sea (Jordán, 1982; Pauly and Tsukayama, 1987), which can be considered a stabilizing factor for the small cetaceans. Despite this, the uncertainty in food availability brought on by El Niño events (e.g. Arntz and Fahrbach, 1996) sums a selection pressure that would compell small cetaceans to acquire an opportunistic feeding strategy.

In conclusion, the high level of sympatry among the four species studied is reflected in their diets. Nevertheless, some differences in its feeding habits can be noted. The Burmeister's porpoise feeds closer to shore in shallower water than the other species, however it is still thought it can forage near the bottom of coastal waters. The distribution range of dusky dolphin and long-beaked common dolphin largely overlap. Despite both species showing a neritic component in their distribution and diet, dusky dolphins are confined exclusively to

pelagic coastal waters, while the bathymetric distribution of prey species suggests that long-beaked common dolphins may dive deeper for food. Along the Peruvian coast the dusky dolphin distribution is strongly linked to cool water and may migrate southward only when a severe El Niño phenomenon occurs (Van Waerebeek, 1992; García-Godos, 1993). The long-beaked common dolphin is thought to exhibit a higher mobility and migrate opportunistically along the west coast of South America. The offshore bottlenose dolphins studied originated mainly from oceanic waters at or beyond the continental slope, which was reflected in a different diet.

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